

A review of the crag lizards (Genus *Pseudocordylus*) of Natal

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INTRODUCTION

It is a pleasure to make a contribution to this volume of the Annals of the Natal Museum, issued in commemoration of the retirement of Dr R. F. Lawrence. It is most fitting that this paper should deal with some Natal representatives of the family Cordylidae, for Dr Lawrence has always been particularly interested in these lizards and has collected much valuable material during his field trips in search of invertebrates.

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The Crag-Lizards of Natal have been a controversial group for many years. *Pseudocordylus subviridis* A. Smith was described from the Natal Drakensberg in 1838 and for over a century all Natal material was referred to this form. In 1943 FitzSimons described *P. subviridis transvaalensis* from the Transvaal Drakensberg.

Loveridge revised the family in 1944 and synonymised *subviridis* and *transvaalensis* with *melanotus* A. Smith (1838), which has page preference. He treated *melanotus* as a race of *P. microlepidotus* of the Cape Province, and described *P. langi* from Mont-aux-Sources with only a single specimen before him. A series in the Transvaal Museum were listed as 'paratypes' on the basis of data supplied by FitzSimons. The original plates illustrating Smith's types of *Pseudocordylus* were reproduced in Loveridge's paper, but unfortunately the caption for Plate 8, fig. 3 was transposed with that for Pl. 9, fig. 2 and for Pl. 10, fig. 2 transposed with that for Pl. 11, fig. 1.

In 1947, FitzSimons described another new species from the Natal Drakensberg—*P. spinosus*. Finally, in 1948, FitzSimons synonymised *P. langi* with *P. s. subviridis*, pointing out that the 'paratypes' were clearly conspecific with the types of *P. subviridis* figured by Smith.

While studying at the University of Natal in 1962, I took the opportunity of examining all the specimens of *Pseudocordylus* in the Natal Museum, Durban Museum and the Natal University Museum. Three weekends were spent in the Cathedral Peak area of the Drakensberg and 48 specimens of *Pseudocordylus*, representing three

species, were collected. At the Transvaal Museum, I examined the type series of *P.s.transvaalensis* and *P.spinosus*, well as as the 'paratypes' of *P.langi*.

After studying most of the available Natal material, it is now possible to distinguish four local forms:

Pseudocordylus spinosus FitzSimons

Pseudocordylus subviridis subviridis (A. Smith)

Pseudocordylus subviridis transvaalensis FitzSimons

Pseudocordylus langi Loveridge.

It has been decided to restrict the scope of this paper to the Natal forms as there is at present insufficient material from the northern Cape Province to make a comprehensive generic revision possible.

Loveridge (1944) transferred *Cordylus capensis* and *C.robertsi* to the genus *Pseudocordylus* and considered them to be closely related to *P.langi*. The resemblances between these forms appears to be due to convergence rather than monophyletic origin. Loveridge's action does draw attention to the artificial nature of the division between *Cordylus* and *Pseudocordylus*. The latter retains its status as a full genus largely because of its convenience.

I am grateful to Drs R. F. Lawrence and V. F. M. FitzSimons for facilities granted at the Natal and Transvaal Museums and Mr W. Lawson for sending me the relevant Durban Museum material on loan. Thanks are also due to the Chief Regional Forestry Officer of Natal for permission to collect in the Cathedral Peak Forest Reserve and to his staff for assistance in the field.

The following abbreviations are used in the systematic discussion: DM=Durban Museum; MCZ=Museum of Comparative Zoology (Harvard); NM=Natal Museum; NUM=Natal University Museum; TM=Transvaal Museum; UM=Umtali Museum.

KEY TO THE GENUS *PSEUDOCORDYLUS*

1. Frontonasal small, longer than broad and well separated from the loreals; lateral scales juxtaposed, strongly keeled and spinose; femoral pores 3-5 *spinosus*
- Frontonasal large, at least as broad as long and making good contact with the anterior loreals; flanks covered with granules, with or without rows of smooth or feebly keeled scales; femoral pores 5-17 2
2. Flanks covered with subuniform granules; lower labials 5; femoral pores 11-17 *langi*
- Flanks covered with scales, separated by granular interspaces; lower labials 6; femoral pores 5-10. 3
3. Upper row of temporals greatly enlarged and vertically elongate; usually 4 upper labials anterior to subocular 4
- Temporals small, polygonal and irregularly arranged; usually 5 upper labials anterior to subocular *microlepidotus*

Form	Series	Supraciliaries	Upper labials anterior to subocular	Lower labials	Gulars transversely between posterior sublinguals	Occipitals	Longitudinal rows of dorsals	Longitudinal rows of ventrals	Transverse rows of ventrals	Femoral pores	Lamellae under fourth toe
<i>P. spinosus</i>	41	4(5)	(3)4	(5)6(7)	16—22	0	32—34	10	28—33	3—5	17—19
<i>P. s. subviridis</i>	98	4(5)	(3)4(5)	(5)6(7)	20—29	(0)8—13	30—44	(10)12(14)	29—36	5—9	19—26
<i>P. s. transvaalensis</i> . .	30	4	(3)4(5)	(5)6	19—26	(0)8—11	32—46	12	29—36	5—10	18—23
<i>P. langi</i>	16	4(5)	4	5	20—27	0	6—8	10—12	32—38	11—17	21—27

Table 1. Variation in the Natal forms of *Pseudocordylus*, unusual variations in parentheses.

4. Lateral scales smaller than the vertical interspaces between them

.. .. . *subviridis subviridis*

- Lateral scales larger than the vertical interspaces between them

.. .. . *subviridis transvaalensis*

Note.—I am unable to investigate the status of the three races of *P. microlepidotus* at the present time. *P. m. namaquensis* is very poorly known and may prove to be linked with *P. m. fasciatus* by a geocline when material is available from the Graaff Reinet area.

SYSTEMATIC DISCUSSION

Pseudocordylus spinosus FitzSimons

Pseudocordylus spinosus FitzSimons, 1947, p. 116, fig. 1; Plate I, figs 5 & 6:
Cathkin Peak area, Drakensberg, Natal.

Variation (41 specimens): Rostral well separated from the small frontonasal, which is diamond-shaped, longer than broad, and well separated from the loreals, making contact with (26 specimens) or separated from (12) the frontal (frontonasal absent in two paratypes, NM. 550 & 555, from Giants Castle); occipitals absent; supraciliaries 4 (78 sides), vary rarely 5 (3 sides); vertically elongate enlarged temporals 3-5; upper labials anterior to median subocular 3 (17 sides) or 4 (65 sides); lower labials 6 (78 sides), very rarely 5 (1 side) or 7 (3 sides); gulars smooth, the lateral rows enlarged, 16-22 rows between posterior sublabials.

Dorsum covered with small, close-set, keeled scales forming regular longitudinal and transverse rows, 32-34 longitudinal rows at midbody; strongly keeled lateral scales directed outwards to form small spines. Scales beneath fore-limbs obtusely keeled; lateral spines on tail well developed, projecting at an angle of 45°. Ventrals smooth, in 10 longitudinal and 28-33 transverse rows; femoral pores 3-5, present in both sexes; lamellae under fourth toe 17-19.

Colouration.—Dark brown above, with pale elongate spots forming irregular longitudinal rows; pale brown below, with a pair of parallel grey longitudinal lines on median gulars.

Size.—Largest ♂ (NUM 73) 214 (89+125) mm. from Royal Natal National Park.

Largest ♀ (TM 21265 199) (89+110) mm. from Cathkin Peak.

Habitat.—This species is found under stones and in rock crevices, frequently in association with the 'montane' form of *Mabuya striata*, on the lower slopes of the Natal Drakensberg at altitudes between 5,000 and 8,000 feet.

Breeding.—A ♀ from Champagne Castle contained a single large embryo in January, other females contained 2 or 3 eggs or embryos.

Diet.—Seven stomachs were examined; these contained small beetles, cockroaches, lepidopterous larvae, a cricket, an ant and a small millipede.

Distribution.—Lower slopes of the Natal Drakensberg from the Royal Natal National Park to Giants Castle.

Localities.—Royal Natal National Park (Dooley Ridge) (NUM, TM & UM); Cathedral Peak (NM, NUM, TM & UM); Cathkin Peak (NM & TM); Champagne Castle (NM); Giants Castle (NM & TM).

Pseudocordylus subviridis subviridis (A. Smith)

Cordylus (*Pseudocordylus*) *melanotus* A. Smith (part, ♀ cotype only), 1838, p. 32: 'Cape of Good Hope', subsequently given as hills between the main branches of the Orange River east of Phillipolis, Orange Free State.

Cordylus (*Pseudocordylus*) *sub-viridis* A. Smith, 1838, p. 33: 'Cape of Good Hope', subsequently given as summit of the Drakensberg behind Kaffirland and Natal.

Cordylus microlepidotus A. Smith (part), 1843, pl. 25, fig. B; pl. 26; pl. 30, fig. 4.

Pseudocordylus microlepidotus Essex (part), 1928, p. 932; Hewitt (part), 1925, p. 356.

Pseudocordylus microlepidotus subviridis FitzSimons, 1937, p. 266.

Pseudocordylus subviridis subviridis FitzSimons (part), 1943, p. 467; 1948, p. 75.

Pseudocordylus microlepidotus melanotus Loveridge (part), 1944, p. 75.

Pseudocordylus langi Loveridge (except the holotype), 1944, p. 73.

Variation (98 specimens): Rostral usually well separated from the frontonasal (in short contact in 5 specimens only), which is at least as broad as long, makes good contact with the anterior loreals and is well separated from the frontal; usually 8-13 small occipitals, sometimes indistinguishable from the scales on the nape; supraciliaries 4 (192 sides), very rarely 5 (4 sides); vertically elongate enlarged temporals 3-7; upper labials anterior to median subocular 4 (181 sides), very rarely 3 (5 sides) or 5 (10 sides); lower labials 6 (191 sides), very rarely 5 (2 sides) or 7 (3 sides); gulars smooth, anteriorly a few median ones irregularly enlarged, lateral rows strongly enlarged and elongate, 20-29 rows between posterior sublabials.

Dorsum covered with small, flat or raised, subcircular scales, forming 30-44 more or less regular longitudinal rows, set in a matrix of smaller heterogeneous granules. In males the dorso-lateral scale rows are separated vertically by granular interspaces equivalent to twice the width of the scales, in females the scale rows are closer set. The scales in the vertebral region are small, squarish, and juxtaposed. Scales beneath forelimbs smooth; lateral spines on tail well developed, but projecting at a lesser angle than those of *spinosus*. Ventrals smooth, in 12 (very rarely 10 or 14) longitudinal and 29-36 transverse rows; femoral pores 5-10, present in both sexes; lamellae under fourth toe 19-26.

Colouration.—♂♂ Dark olive to black above, snout, labials and flanks pale olive, two black patches on side of neck, dorso-lateral scales black-tipped, forming lines, flanks bright orange in fully adult males. Greenish-white below, sublabials and median gulars suffused with slate grey. Limbs pale olive, blotched with black above. Tail black above, olive to bright orange laterally with vertical black bars, orange below, becoming uniform olive to black towards the tip.

♀ ♀, juveniles and a few ♂ ♂ pale olive above, with darker mottling on the head and a black network on the back, dorsolateral scales black-tipped, forming lines. Pale olive below, the throat suffused with grey. Tail olive, blotched with black above.

Size.—Largest ♂ (UM 2171) 262 (115+147) mm. from Organpipes Pass, but NM 897 from Mont-aux-Sources has a head and body length of 120 mm. Largest ♀ (NM 951) 218 (92+126) mm., but NM 600 from Giants Castle has a head and body length of 96 mm.

Habitat.—This form is abundant in the Natal Drakensberg at altitudes from 5,500 to 11,000 feet. It usually lives in fissures, but may sometimes be found under stones. It is sympatric with *P. langi* at the summit of the Organpipes Pass, where *Tropidosaura essexi* and *T. cottrelli* also occur.

Breeding.—A ♀ from Giants Castle (NM 666) contained 4 well developed embryos in April. Other females contained 2-4 large eggs in April-May.

Diet.—The stomach contents for 22 specimens collected in the Cathedral Peak area (April-May 1962) were analysed. The number of individuals containing various food items was as follows:

Coleoptera (adults)	9
Hymenoptera—Formicoidea	8
Orthoptera	7
Lepidoptera (larvae)	6
Araneida..	3
Lepidoptera (adult moth)	1
Hemiptera	1
Coleoptera (larva)	1
Diptera (larva)	1
Diplopoda	1

Parasites.—Many specimens harboured larval mites, identified by Dr R. F. Lawrence as *Eutrombiculata montensis*; *Euschongastia tropidosauri* and *Schongastia* sp. A few ticks were present. A number of lizards contained nematodes.

Distribution.—Common along the Natal Drakensberg from Mont-aux-Sources to Underberg, extending south through Basutoland to the Amatola Mountains. This form is sympatric with *Pseudocordylus microlepidotus fasciatus* in the north-eastern Cape Province.

Localities (Natal only).—Mont-aux-Sources (NM & TM); Royal Natal National Park (UM); Organpipes Pass, near Cathedral Peak (UM & MCZ); Cathkin Peak (NM); Champagne Castle (NM); Bushman's Peak (NM); Giants Castle (NM, TM & UM); Drakensberg near Underberg (TM).

Remarks.—Loveridge's revival of Smith's name *melanotus* was most unfortunate, but for this action it would now be classed as a *nomen oblitum* under the International Code of Zoological Nomenclature. The types of both *melanotus* and *subviridis* are lost (FitzSimons, 1937). In Smith's figures of the head shields (1843, Plate 30) neither

P.melanotus (fig 3) nor *P.subviridis* (fig. 4) are shown with the elongate temporals typical of the common Basutoland-Natal Drakensberg form, both resemble the types of *P.s.transvaalensis* in this respect. However, Plate 26 clearly illustrates *P.s.subviridis*, with elongate temporals and a uniform black dorsum in the male. Plate 25 (*P.melanotus*) once more shows a male lizard with a typical *P.s.transvaalensis* temporal arrangement, the female has elongate temporals. Unfortunately no material is available from the south-eastern Orange Free State (Rouxville-Zastron area)—type locality of *P.melanotus*, but the Natal Museum has three specimens (NM 551) from Herschel, C.P., just south of the Orange River and only twenty miles from Zastron. The two females are *P.s.subviridis*, but the third lizard is a huge male measuring 315+ (145+170+) mm. The temporal arrangement on one side of the head matches *P.s.transvaalensis*, the temporal area on the other side is covered with scar tissue. This specimen comes closest to *P.microlepidotus fasciatus* and Smith's male cotype of *melanotus* was clearly the same thing, for he gives the length of *melanotus* as 12 to 14 inches (305-355 mm.), whereas the maximum length recorded for *P.s.subviridis* is only 262 mm. The name *melanotus* is here restricted to the male cotype and it is made a junior synonym of *P.m.fasciatus*, which has paragraph preference. It should also be noted that Smith's male cotype of *melanotus* is shown (1843, Plate 30, fig. 3) to have five upper labials anterior to the subocular, a normal arrangement in *P.microlepidotus*, but a rare one in *P.subviridis*.

Pseudocordylus subviridis transvaalensis FitzSimons

Pseudocordylus subviridis transvaalensis FitzSimons, 1943, p. 469: Woodbush, Pietersburg District, N. Transvaal.

Pseudocordylus subviridis subviridis (not A. Smith) FitzSimons (part), 1943, p. 467.
Pseudocordylus microlepidotus melanotus (not A. Smith) Loveridge (part), 1944, p. 75.

Variation (30 specimens).—Rostral usually well separated from the frontonasal (in short contact in 5 specimens only), which is at least as broad as long, makes good contact with the anterior loreals and is well separated from the frontal; usually 8-11 small occipitals, sometimes indistinguishable from the scales on the nape; supraciliaries 4; vertically elongate enlarged temporals 4-6; upper labials anterior to median subocular 4 (55 sides), rarely 3 (2 sides) or 5 (3 sides); lower labials 6 (58 sides), very rarely 5 (2 sides); gulars smooth, anteriorly a few median ones irregularly enlarged, lateral rows strongly enlarged and elongate, 19-26 rows between posterior sublabials.

Dorsum covered with moderately large scales, which are flat and squarish on the vertebral line, subcircular and raised, feebly ribbed or obtusely keeled laterally, forming 32-46 regular rows, set in a matrix of heterogeneous granules. The scales are close-set, often juxtaposed vertically, the gap between them not exceeding their own width. Scales beneath fore-limbs smooth to feebly keeled; lateral spines on

tail as in typical *subviridis*. Ventrals smooth, in 12 longitudinal and 29-36 transverse rows; femoral pores 5-10, present in both sexes; lamellae beneath fourth toe 18-23.

FitzSimons (1943, p. 463) provided the following key to the races of *P. subviridis*:

A single row of large vertically elongate temporals; lowermost temporal spine moderately projecting in males. *P. s. subviridis*

Two rows of temporals, the upper vertically elongate and much larger than the subhexagonal lower; lowermost temporal spine feebly projecting and only bluntly pointed *P. s. transvaalensis*

Loveridge (1944) found that these characters were variable in the material which he had before him and this led him to synonymise *transvaalensis*. Actually there is an *average* difference in the temporal arrangement of northern and southern populations of *subviridis* and it may be possible to plot a character gradient, but the nature of the dorsolateral scalation provides a more stable character on which to base a northern race.

Colouration.—Olive to dark brown above, head mottled darker; usually with well-defined pale dorsal blotches, which tend to form irregular cross-bands; flanks usually pale olive, suffused with orange in adult males and some females, with dark vertical bars. Cream to pale olive below, often suffused with pale orange laterally, throat suffused with slate grey. Tail blackish, blotched with pale olive dorsally, often ringed with black and orange at the base, becoming uniform black distally.

Size.—Largest ♂ (NM 1330) 239 (107+132) mm., from Van Reenen, but NM 808 from Pietermaritzburg measures 121 mm. from snout to vent (tail truncated). Largest ♀ (NM 997) 262 (115+147) mm. from Qudeni Forest, north of Greytown.

There appears to be a geocline in the average size of this form. The largest specimens are recorded from Woodbush—the cotypes measure ♂ 327 (151+176) mm., ♀ 305 (134+171) mm. Populations become progressively smaller in size as one travels further south, until those in the Natal midlands average only a little larger than *P. s. subviridis*.

Habitat.—This form is found in isolated colonies on suitable rock outcrops throughout the Natal midlands. It is very common near Nottingham Road, where the road to Underberg is cut into the hillside, leaving a jumble of rock at the roadside. A *Pseudocordylus* may be seen basking on nearly every prominent rock.

Breeding.—Two females each contained four eggs.

Diet.—Three specimens collected in March at Dansekop and Nottingham Road contained numerous lepidopterous larvae, beetles, winged termites and a grasshopper.

Distribution.—Pietermaritzburg, north through the Natal midlands, north-eastern O.F.S. and western Swaziland to the Transvaal Drakensberg.

Localities (Natal only).—Swartkops, Pietermaritzburg (NM); Pietermaritzburg (NM); Lidgetton (NM); Nottingham Road (UM); Willbrook, near Estcourt (DM); Dargle (NM); Dansekop (UM); Qudeni Forest, north of Greytown (NM); Van Reenen (NM & DM); Muller's Pass, Newcastle (NM); Botha's pass, Newcastle (NUM & UM).

Pseudocordylus langi Loveridge

Pseudocordylus langi Loveridge (holotype only, the remainder *P.s.subviridis*), 1944, p. 73: Mont-aux-Sources, Drakensberg.

Pseudocordylus subviridis subviridis (not A. Smith) FitzSimons, 1948, p. 75 (holotype of *P.langi* only).

Variation (16 specimens).—Rostral well separated from the frontonasal (but nasals separated by an azygous shield in UM 2412), which is much broader than long, making good contact with the anterior loreals, well separated from the frontal (frontonasal longitudinally divided in UM 2413 and 2418); prefrontals in broad contact, except in UM 2412, where they are separated by a narrow azygous shield; frontal and frontoparietals very variable in size and shape; occipitals absent; supraciliaries 4 (28 sides), rarely 5 (4 sides); vertically elongate enlarged temporals 4-6; upper labials anterior to median subocular 4; lower labials 5, due to fusion of the sixth lower labial with the fifth (posterior) sublabial; gulars smooth, elongate, less variable in size than in *P.subviridis*, 20-27 transversely between posterior sublabials.

Dorsum with a vertebral band of small, squarish, smooth, juxtaposed scales, forming 6-8 longitudinal series; rest of dorsum and flanks covered with small homogeneous granules, which also cover the underside of the forelimb. Lateral caudal spines feebly developed and not extending as far down the tail as in *P.subviridis*. Ventrals smooth, in 10-12 (mean=11.0) longitudinal and 32-38 transverse rows; femoral pores 11-17, very small, present in both sexes; lamellae under fourth toe 21-27.

Dr E. E. Williams has kindly compared one of my Organpipes Pass series with the holotype of *P.langi* in the Museum of Comparative Zoology (Harvard) and found them to agree in all diagnostic characters.

Colouration (from life).—Head olive grey, heavily blotched and streaked with black, particularly in the parietal region; back olive grey, heavily streaked with black and often with numerous pale grey-green blotches, which tend to form cross-bands; two large black patches on the side of the neck (separated by a light grey fold of skin) extending to above the shoulder, followed by a series of 1-6 bright sky-blue spots, which form a lateral series (this vivid colouration rapidly fades after death); upper surface of limbs and tail olive grey, variegated with black and pale grey-green.

Below, chin and throat white, lower labials and chin infusate; median gulars with a large dark brown patch, flanked on each side by three parallel narrow brown lines; chest, belly and undersurfaces of limbs slate grey, dark spotted, belly and anal region of one male (UM 2414) suffused with dull orange, but this colouration does not extend onto the flanks as in *P.subviridis*; tail pale olive grey below.

Size.—Largest ♂ (UM 2411) 252 (106+146) mm. from Organpipes Pass, near Cathedral Peak, Natal Drakensberg. Largest ♀ (UM 3012) 202 (83+119) mm.,

but exceeded in head and body length by UM 2415, which measures 186 (86+100) mm. Both from Organpipes Pass.

Habitat.—In the Cathedral Peak area *P. langi* lives in fissures at an altitude of about 8,500 to 10,000 feet. It is usually found by itself in small colonies, but at the summit of Organpipes Pass it lives in the same crevices as *P.s.subviridis*. A few specimens were found under stones in areas frequented by *Tropidosaura cottrelli*.

Breeding.—Two eggs, measuring 5 x 5 mm., were found in the ovaries of UM 2415 (12.v.62).

Diet.—The stomach contents of 12 specimens collected in the Organpipes Pass on 12-13 May, 1962, were analysed. The number of individuals containing various food items was as follows:

Vegetable matter (leaves, flower petals) ..	5
Hymenoptera—Formicoidea	5
Orthoptera—Acridiidae	4
Coleoptera (adults)	4
Araneida	2
Lepidoptera (larvae)	2
Orthoptera—Blattidae	1
Hymenoptera—Ichneumonoidea	1

The lizards which contained vegetable matter had eaten the leaves of a number of different Compositae, but the fragments were too macerated to be identifiable even to genus. One lizard had eaten the yellow 'rayed' petals of an 'everlasting' (*Helichrysum* sp.), which grows in fissures on the lava rock faces where *P. langi* is found.

Parasites.—No mites were found on this species but ticks were removed from the neck and throat of two specimens. Nematodes were found in the stomach and rectum of two lizards.

Distribution.—Apparently restricted to the summit of the Natal Drakensberg (i.e. along the Basutoland border) between 8,500 and 11,000 feet, but far less common than *P.s.subviridis* and local in distribution.

Localities.—Mont-aux-Sources (MCZ); Organpipes Pass, near Cathedral Peak (UM, MCZ, NM & TM).

'CENTRIFUGAL EVOLUTION' IN *PSEUDOCORDYLUS*

Although much work remains to be done on *Pseudocordylus*, particularly with regard to the poorly known forms of the northern Cape Province (*P.microlepidotus fasciatus* and *P.m.namaquensis*), it is now possible to outline the possible course of evolution in this genus.

The evolutionary centre for *Pseudocordylus* was the Natal-Basutoland section of the Drakensberg, particularly the north-eastern escarpment. Only here do three species occur together. The lava ramparts of the 6,000 foot high escarpment provided

Pseudocordylus with an ideal habitat, and climatic changes could be easily circumvented by movement up and down the steep slopes. Populations left behind and isolated by these movements have diverged to give rise to *P. langi* at the summit and *P. spinosus* at the lower levels.

A hypothetical ancestor of *Pseudocordylus* had a range extending from the south-western Cape along the eastern escarpment to the N.E. Transvaal. This ancestral form was a large lizard, with numerous small temporals, probably little different from the present forms of *P. microlepidotus*. During dry periods *Pseudocordylus* would be restricted to the summits of the higher mountain ranges, gene flow between populations would be interrupted, and the isolated groups would diverge. The central (Basutoland) group always had the largest area of suitable temperate habitats and therefore the largest populations and the most rapid rate of evolution. These Basutoland lizards gradually became smaller in size (a common evolutionary trend) and the small temporals fused to form elongate shields. During pluvial periods there was enough intermittent gene flow between the central and northern populations to prevent them diverging beyond the subspecific level, but by the time the central and southern populations came into contact again they had diverged to a point where they were reproductively isolated, giving rise to two sympatric species in the north-eastern Cape Province.

The evolutionary pattern exhibited by *Pseudocordylus* is one of 'centrifugal speciation' (W. L. Brown, 1957). The forms at the periphery of the generic range (*P. microlepidotus* and the Woodbush populations of *P. s. transvaalensis*) resemble each other (and the ancestral form) in their large size and numerous temporals (this character partially obscured in *P. s. transvaalensis* by intermittent contact with *P. s. subviridis*). The three forms left at the evolutionary centre (*P. spinosus*, *P. s. subviridis* and *P. langi*) are the most advanced, they are also the three smallest forms and all three have large, vertically elongate temporals.

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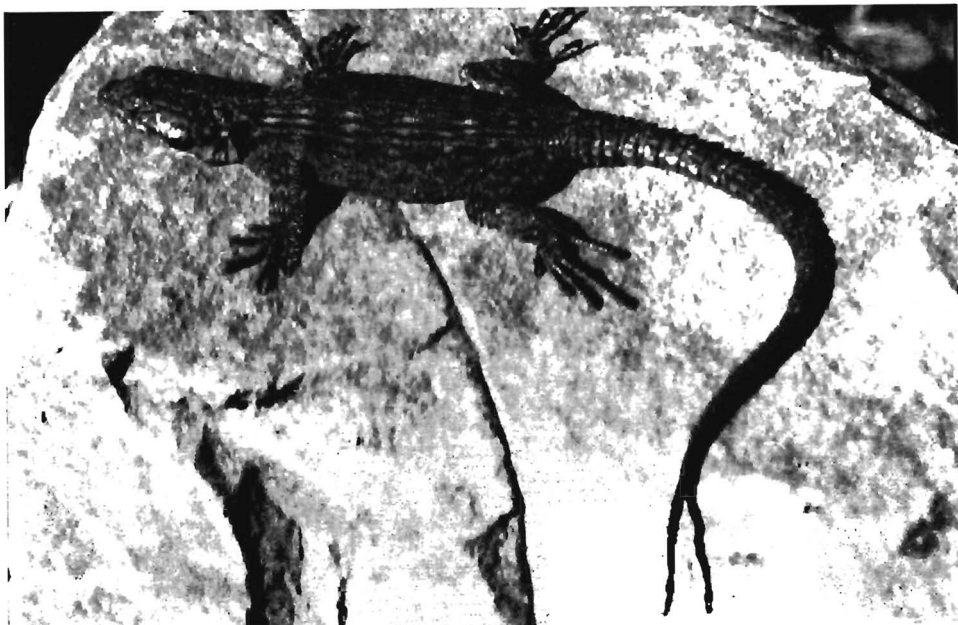


Fig. 1.—*Pseudocordylus langi*, female, Organpipes Pass, Cathedral Peak, Natal Drakensberg.



Fig. 2. —Organpipes Pass, Cathedral Peak, Natal Drakensberg.
Habitat of *Pseudocordylus langi*.